Trial history effects in the ventral attentional network

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Abstract

The ventral attentional network (VAN) is thought to drive "stimulus driven attention"(e.g. Asplund et al., 2010; Hulman et sl., 2003); in other words, it instantiates within the current stimulus environment the top-down attentional biases maintained by the dorsal attention network (e.g. Kincade et al., 2005). Previous work has shown that the dorsal attentional network is sensitive to trial history, such that it is challenged by changes in task-goals and facilitated by repetition thereof (e.g. Kristjansson et al., 2007). Here, we investigate whether the VAN also preserves information across trials such that it is challenged when previously rejected stimuli become task relevant. We used fMRI to investigate the sensitivity of the ventral attentional system to prior history effects as measured by the distractor preview effect (DPE). This behavioral phenomenon reflects a bias against stimuli that have historically not supported task performance. We found regions traditionally considered to be part of the VAN (right middle frontal gyrus, inferior frontal gyrus and right supramarginal gyrus; Shulman et al., 2003) to be more active when task-relevant stimuli had not supported task performance in a previous trial than when they had. Investigations of the ventral visual system suggest that this effect is more reliably driven by trial history preserved within the VAN than that preserved within the visual system per se. We conclude that VAN maintains its interactions with top-down stimulus biases and bottom-up stimulation across time, allowing previous experience with the stimulus environment to influence attentional biases under current circumstances.

Introduction

"Everyone knows what attention is...it implies withdrawal from some things in order to deal effectively with others" (James, 1890). When we approach the busy visual world with the goal of "effectively dealing" with particular visual stimuli, we direct attention in exactly the manner described by James (1890): information that will lead to an appropriate response is prioritized over that that will not. This prioritization is widely believed to reflect the biasing of perceptual processing systems to favor material that will support current processing goals at the expense of material that will not; these biases have their source in a broadly distributed network of frontal and parietal regions (Desimone & Duncan, 1995). A dorsal attentional network that includes the frontal eye-fields (FEF) and the superior aspect of the intra-parietal sulcus (IPS) maintains attentional biases towards information that supports current task goals (Kincade et al., 2005; Szczepanski et al., 2010, 2013; Kastner et al., 2007). Successful attentional function, however, requires not only that biases towards task-relevant material be generally maintained across task conditions; but also they will interact with the specific context of the current stimulus environment. Sometimes called "stimulus driven attention"(e.g. Asplund et al., 2010), this function is subserved by a ventral network that includes the right middle frontal gyrus, inferior frontal gyrus and right superior parietal sulcus/temporal parietal junction (Shulman et al., 2003; Corbetta et al., 2008; Shulman et al., 2007; Todd et al., 2005, Asplund et al., 2010; Serences et al., 2005). Together, the dorsal and ventral attentional networks interact to maintain attentional biases appropriate to task goals and apply them to the current physical environment.

Behavioral evidence suggests that when attentional biases are instantiated in response to specific stimuli, they persist beyond any individual trial. Search for even a highly salient "pop-out" target presented among distractors is facilitated if that target repeats the defining feature of

that of the previous trial (e.g., Maljkovic & Nakayama, 1994). The phenomenon, known as "priming of pop-out" (POP), is thought to reflect a positive bias in favor of conditions that previously produced successful task performance (e.g., Huang, Holcombe & Pashler, 2004; Maljkovic & Nakayama, 1996; Wolfe, Butcher, Lee & Hyle, 2003). Conversely, search for a highly salient pop-out target presented among distractors is inhibited if that target shares defining features with items in a prior trial that contained no target at all (and thus resulted in a "failed" search; e.g., Ariga & Kawahara, 2004; Goolsby, Grabowec ky & Suzuki, 2005; Lleras, Kawahara, Wan & Ariga, 2008). This phenomenon is known as the "distractor preview effect" (DPE) and is thought to reflect a bias against stimuli that do not support task performance. Despite its name, the DPE in fact derives from the cost of orienting towards a target item that has the same features as recent non-targets rather than a benefit of orienting away from distractor features that have recently been ignored (Caddigan & Lleras, 2010; LLeras et al., 2009). Both phenomena illustrate the tendency of biases within the attentional system to persist across trials, even under circumstances in which attentional selection should be effortless and automatic (pop-out search).

Attentional biases in favor of task-relevant information are generally thought to be instantiated and maintained by the dorsal attentional system (Kincade et al., 2005; Szczepanski et al., 2010, 2013; Kastner et al., 2007; Zhou & Desimone, 2011). Trial history effects have been found within the dorsal attentional systems of both human and non-human primates (Kristjansson et al., 2007;Bichot & Schall, 1999; 2002); this system is generally more challenged (or less efficient) if the specific stimulus characteristics consistent with task goals vary from trial to trial. For example, MEG (Astle et al., 2012), fMRI (Manoach et al., 2007) and single cell methodology (Bichot & Schall, 1999) demonstrate that demands on the frontal eye fields are

higher when task goals switch rather than remain constant between trials. Data collecting during a POP paradigm reveals similar results; recruitment of FEF and IPS is increased when the pop-out target on the current trial shares no relevant dimensions with the target of a previous trial (Kristjannson et al., 2007). The state of the dorsal attentional network on any given trial, then, is at least partially preserved through the subsequent trial; this reduces the demands placed on the system should target features or task requirements remain constant across trials, but increases them should target features or task requirements vary between trials.

The ventral attention network appears to support the appropriate application of attentional biases to the specific stimulus environment. It is particularly taxed by conditions that require the adjudication of the target status of stimuli whose features partially overlap with task-goals and expectations (Shulman et al., 2003; Corbetta et al., 2008; Shulman et al., 2007, Corbetta et al., 2000,). It is also active when distractor items have a high potential to draw attention away from a task-relevant item (Serences et al., 2005; Asplund et al., 2010; Susuki et al., 2012). Conversely, temporary deactivation of this network leaves task performance vulnerable to disruption by salient non-target items (Suzuki et al., 2012). When distractor items are absent or have low potential to interfere with target identification, this network is comparatively silent (Shulman et al., 2003; 2007, Todd et al., 2005; Suzuki et al., 2012). The ventral attention network, then, appears to be recruited to evaluate the concordance between attentional biases in favor of task relevant material and the extant stimulus environment. It plays a crucial role in identifying target information that is highly similar to distracting or non-target information.

How then might trial history influence the action of the ventral attentional system? We suspect that the ventral attentional system will be particularly sensitive to prior history with non-target material, such that identifying it as non-target information re-aligns attentional biases for

the subsequent trial. Specifically, when previous non-target material maintains its non-target status, stimulus conditions should be well aligned with previously instantiated attentional biases (i.e. items that were previous rejected should continue to be rejected), and the ventral attentional system should be relatively silent. When previous non-target material becomes the target, however, stimulus conditions should be relatively poorly aligned with previously instantiated attentional biases (i.e. material that was formerly rejected must now be selected), and the ventral attentional system should be recruited to mediate these circumstances.

In the current experiment, we used fMRI to investigate the sensitivity of the ventral attentional system to prior history effects as measured by the DPE. In this experiment, participants responded to the right/left location of a dot with respect to a categorical oddball (face/house). We examined blood oxygen-level dependent (BOLD) response to trials that contained such an oddball. We compared trials preceded by two types of no-target (i.e. target-absent) trials: those that contained members of the current target category (target preview) to those that contained members of the current distractor category (distractor preview). Consistent with prior behavioral findings (e.g., Buetti & Lleras, submitted; for a temporal version of the task see Levinthal & Lleras, 2008b; Lleras, Kawahara & Levinthal, 2009; for a review see Lleras, Levinthal, & Kawahara, 2009), we predicted a robust preview effect; trials whose targets matched the category of items that occurred on the preceding no-target trial (target preview) were responded to more slowly than those whose distractor matched the category of items that occurred on the preceding no-target trial (distractor preview). This slowed performance is thought to reflect changes in the difficulty of selecting target material that was rejected on the prior non-target trial (Lleras et al., 2009); the ventral attentional system, then, should be especially challenged by these conditions (e.g. Shulman et al. 2003; 2007). Such a finding

would indicate that prior history does indeed influence the ongoing action of the neural system that responds to the alignment between the current stimulus settings with current attentional biases.

We also exploited our design to expand our understanding of the DPE per se; although the DPE is generally believed to reflect biasing of the attentional system, it could also be explained by pre-attentive perceptual mechanisms (Goolsby et al., 2005). According to this hypothesis, attention-related suppression of a task-relevant stimulus attribute in a no-target trial persists to subsequent trials, making encoding of that stimulus attribute more difficult than it would have been had suppression not occurred. Under such conditions, performance would be impaired on trials for which the current target had been suppressed on the prior no-target trial, whereas performance would be facilitated on trials for which the current distractor had been suppressed on the prior no-target trial. The categorical distractor preview task that we employ in this experiment allows us to interrogate category sensitive regions in the ventral visual stream (the fusiform face area (FFA) and parahippocampal place area (PPA)) for such persistent sensory suppression. Specifically, if sensory suppression persists across trials, we should find activation in FFA to be suppressed on trials preceded by no-target face trials rather than no-target house trials and activation in PPA to be suppressed on trials preceded by no-target house trials rather than no-target face trials. Note that previous efforts to find evidence of preview related persistent sensory suppression have been unsuccessful; the N180, an event-related potential component associated with the relative salience of perceptual features is insensitive to the relationship between the target and distractor features of a current trial with those of a preceding no-target trial (Shin et al., 2008). Consequently, we do not expect to find evidence of persistent sensory suppression in the current experiment. The relatively poor spatial resolution of ERP

techniques, however, may have obscured highly localized suppression of sensory processing. In the current experiment, we exploit the high spatial resolution of fMRI to identify category sensitive regions in each participant and interrogate them for any suppressive effects associated with trial history.

Methods

Behavioral Methods

Participants: We collected data from 16 volunteers with normal or corrected-to-normal vision who participated in the experiment for financial compensation. All participants gave informed written consent. Data from one participant were excluded because he misunderstood the task instructions. Data from two subjects were excluded due to extremely low accuracy (66% or less in any condition), which would have compromised the number of trials available for fMRI analysis. The study was approved by the University of Illinois Institutional Review Board.

Task and Trial Design: A small white donut appeared in the center of the screen at the beginning of each run. Participants were told that the task would be easiest if they kept their eyes fixed on this stimulus throughout the run. After a 15 second delay (included to allow longitudinal magnetization to approach equilibrium before data collection began), 200 ms search displays appeared at variable interstimulus intervals. ISI's were pseudo-randomly distributed throughout each run: there were 54 possible ISIs in the range 3000-5650ms (in 50ms steps) all equally likely, and each was used twice during each run. This "jitter" in the ISI aided deconvolution of the task-related hemodynamic response functions (HRF) during data analysis. Each search display contained three pictures arranged in an invisible iso-acuity ellipse (5°x4°) centered around the fixation stimulus. Each triangle contained one picture above fixation and two pictures

below fixation (see figure 1). Pictures subtended 2.86 ° X 2.86° of visual angle. Pictures were drawn without replacement from a collection of face and house images. A small red dot (approximately 0.34 °) was placed .51° to the right or left of the center each picture. Participants were to find the categorical "oddball" image in the display and report the relative location of its red dot (right vs left of the object center). For example, a face picture presented with two house pictures would have been an oddball, and participants would have indicated whether the red dot on this picture appeared on its right or left side of the face. Oddballs appeared only below fixation (Kristjansson et al. 2007; Kristjansson et al., 2005). Participants indicated their responses by pressing one of two keys on a button-box. In approximately half of the trials, all three pictures belonged to the same category (i.e. target-absent trials). If participants did not find a target, they pressed a third key on the button box. Participants were asked to respond as quickly and accurately as possible.

Experimental Design: Each participant performed a practice block of 24 trials during scanning, then completed 6 blocks of 108 trials. Trials were equally divided among "all faces", "all houses", "face target" and "house target" configurations. Because we were specifically interested in behavior and brain activity associated with target-present trials that followed target-absent trials, 80% of trial pairs followed this pattern. 50% of these pairs "previewed" the target, while the remaining 50% "previewed" the distractor. The remaining 20% of trial pairs contained either two consecutive target-absent trials or two consecutive target-present trials.

Localizer Task: After completing the main experiment, participants completed a single block of localizer scanning. Participants maintained fixation on the fixation dot at the center of the screen and passively viewed displays of three pictures from the same (either face or house) category, presented in the same configuration as the main experiment. For ten participants each display

was presented for 500 ms, for six participants each display was presented for 1000 ms. As in the main experiment, display ISIs ranged from 3000 to 5650 ms. Displays of a specific category were successively repeated 20 times, followed by 20 displays of the other category. This alternation repeated seven times.

Equipment: MATLAB with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) run on an HPdc7900 SFF-SRP US (operating system; windows XP) controlled experiment presentation and response collection. Stimuli were presented via back projection (Brain Logics, Psychology Software Tools). Responses were collected using a USB MRI compatible response box (Brain Logics, Psychology Software Tools).

Neuroimaging Methods

Data Acquisition and Analysis: Imaging data were acquired in a 3-T scanner (Trio, Siemens) using a 12-channel head coil. We acquired high resolution EPIs (TR = 2.5 s; TE = 25ms; flip angle = 90 º; matrix =120 X 110; voxel size = 2.13 X 2.13 X 2.4, 1.2 mm gap; FOV=256 X 236) in 42 interleaved axial slices. We collected 6 experimental runs of 209 repetitions. We also collected a localizer run of 204 repetitions for 10 participants and 267 repetitions for 6 participants. The localizer scan of one participant to terminate early due to scanner operator error; this participant showed above threshold differences for the two categories in the expected regions, so we included his data in subsequent analysis. To assist in registering EPI images to anatomical space, we collected T2 weighted anatomical images (TR=6100ms; TE = 93 ms; flip angle =150º; 256 X 236 matrix) with 42 ascending axial slices. We also collected high-resolution T1 anatomical images (MPRAGE; FOV = 230mm X 230 mm, matrix =512 X 512; TR = 1900 ms, TE = 2.32 ms; voxel size = .45 X .45 X .9 mm).

We used FMRIB (Oxford University Centre for Functional MRI of the Brain) Software Library (FSL) to analyze our functional data. Data were brain-extracted, high-pass filtered (sigma = 15 seconds), intensity normalized and motion corrected [FSL 4.1.9, (Smith et al., 2002; Jenkinson et al., 2002)].

Individual subject analysis procedures: We concatenated data across all six runs, and submitted them to GLM analysis using FEAT (FMRI Expert Analysis Tool) v 5.98 [FSL 4.1.9; (Smith et al., 2004; Woolrich et al., 2001)]. We modeled six regressors of interest (3 Faces, 3 Houses, Face Target preceded by 3 Faces, Face Target preceded by 3 Houses, House Target preceded by 3 Faces, House Target preceded by 3 Houses) and two regressors of no interest (target present trials preceded by other target present trials and errors). All regressors were convolved with a double-gamma model of the HRF (Phase 0s). Motion correction estimates were also modeled as regressors of no interest. We calculated contrast parameter estimates for all target preview trials relative to all distractor preview trials, all face targets previewed by faces with face targets previewed by houses (face target preview vs face distractor previews) and all house targets previewed by houses relative to all house targets previewed by faces (house target preview vs house distractor preview). The resulting statistical maps for each parameter estimate and contrast parameter estimate were registered into the participant's individual anatomical space and into standard space using *FMRIB's Linear Image Registration Tool (*FLIRT; Jenkinson et al., 2002).

Whole Brain Analysis Procedures: The statistical maps for each contrast parameter estimate of interest were fed into separate random-effects group analyses by *FMRIB's Local Analysis of Mixed Effects* (FLAME). FLAME uses Markcov chain Monte Carlo (MCMC) sampling to estimate the true random-effects and degrees of freedom at each variable. As such, it is much more conservative than traditional mixed-effects analysis. Clusters of voxels with z-scores above

2.3 and more than 1000 voxels (cluster p <.01; number of clusters = 2) or with a z-score above 3 (uncorrected voxel p <.001; number of clusters =1) were labeled significant.

Ventral Visual Stream Analysis Procedures: We used the localizer procedures described below to identify bilateral FFA and bilateral PPA in each participant. We projected each participant's ROIs into individual anatomical space. We then used Featquery (Smith et al., 2004) to extract the weighted percent signal change for each of the 6 experimental regressors of interest (3 Faces, 3 Houses, Face Target preceded by 3 Faces, Face Target preceded by 3 Houses, House Target preceded by 3 Faces, House Target preceded by 3 Houses). Featquery applied the MPRAGE to EPI transformation matrix calculated during image registration to determine which EPI voxels fell within the ROI (selected in MPRAGE space).

Localizer data analysis: We submitted data to GLM analysis using FEAT v 5.98 [FSL 4.1.9; (Smith et al., 2004; Woolrich et al., 2001)]. We modeled two regressors of interest (3 Faces, 3 Houses). All regressors were convolved with a double-gamma model of the HRF (Phase 0s). Motion correction estimates were also modeled as regressors of no interest. We also calculated the contrast parameter estimate for houses relative to faces. The resulting statistical maps were registered into the participant's individual anatomical space and into standard space using FLIRT (Jenkinson et al., 2002). PPA was identified in each hemisphere by identifying the voxel in the temporal parahippocampal gyrus that was maximally selective (highest Z score) for houses relative to faces, then selecting all contiguous voxels whose selectivity for houses was greater than 80% of the maximum z-score. FFA was identified in each hemisphere by identifying the voxel in the temporal fusiform gyrus that was maximally selective for faces relative to houses, then selecting all contiguous voxels whose Z score was greater than 80% of the maximum z-score. One participant failed to show any voxels in the right temporal fusiform gyrus with a z-

score of greater than 2 for the face vs houses contrast; this participant's right fusiform area was not included in the analysis.

Results

Behavioral Analysis:

We submitted reaction time data from each participant to repeated measures ANOVA, using the factors target type (faces, houses) and preview type (faces, houses). The interaction between target and preview type was significant ($F(1,12) = 59.9$; $p = .0$). Reaction time to face targets previewed by house non-targets (1057 ms) was faster than to face targets preceded by face non-targets (1178 ms). Reaction time to house targets preceded by face non-targets s (1067 ms) was faster than to house targets preceded by house non-targets (1182 ms). No other main effects were significant ($p > .74$).

We submitted accuracy data from each participant to repeated measures ANOVA, using the factors target type (faces, houses) and preview type (faces, houses). The interaction between target and preview type was again significant ($F(1,12) = 9.5$; $p = .01$). Accuracy to face targets preceded by house non-targets (85%) was higher than to face targets preceded by face non-targets (82%). Accuracy to house target trials preceded by face non-targets (87%) was greater than accuracy to house target trials preceded by house non-targets (85%). No other main effects were significant ($p > .14$). In sum, we observed a significant categorical DPE on behavior: RTs (and accuracy) were slower (and less accurate) on trials on which the current target belonged to the same category as items on the preceding no-target trial.

Full Brain Analysis

Our primary goal was to determine whether prior experience with a target item increased recruitment of the ventral attentional system. We therefore compared parameter estimates for all trials whose targets (face and houses) had been previewed with those for all trials whose distractors (faces and houses) had been previewed. Significant clusters (Z>2.3, cluster p <.05) of activation that higher for target-previewed trials than for distractor-previewed trials were found in the right middle frontal gyrus (Z>2.3 (peak Z = 3.25); k=1113; cluster p =.016) and the right supramarginal gyrus (Z>2.3 (peak z = 3.18); k=1150; cluster p =.014). No other significant clusters of activation (cluster p <.05) were found.

Ventral Stream ROI analysis; PPA: As mentioned above, the DPE reflects a compromise in the ability of an *attended* item to drive behavior if that item has been rejected on a previous trial; prior suppression of current distractor material does not benefit performance (Caddigan & Lleras, 2010; Lleras, Levinthal & Kawahara, 2009). Preview effects should therefore emerge in the regions active in processing target material. We therefore examined % signal change in left and right PPA for conditions in which houses served as targets (House Target preceded by 3 Faces, House Target preceded by 3 Houses) and compared activity evoked by the two preview conditions (Faces previewed or Houses previewed). Signal did not vary systematically between the left and right PPA for any condition (p >.37), so we collapsed the data across the right and left hemisphere for each condition. We submitted % data from each participant to house target trials to a paired t-test, using the factor preview type (faces, houses). Signal to house target trials preceded by face non-targets (.073%) was no different than to house target trials preceded by house non-targets (.075%) (t(12)=.08; p = .934; see Figure 3).

Ventral Stream ROI analysis; FFA: As in the PPA, we restricted our analysis in the FFA to those conditions in which the target was a face. We examined % signal change for the two face target

conditions (Face Target preceded by 3 Faces, Face Target preceded by 3 Houses) from the left and right FFA. Signal did not vary systematically between the left and right FFA for any condition ($p > .15$), so we collapsed the data across the right and left hemisphere for each condition. We submitted % data from each participant to face target trials to a paired t-test, using the factor preview type (faces, houses). Signal to face targets previewed by house non-targets (.114%) was no different than to face target trials preceded by face non-targets (.116%; $t(12) = .204$; $p = .841$; see Figure 3).

Discussion

We report evidence that the ventral attentional system is sensitive to trial history. Task performance was compromised if the category of the current target item, rather than the current distractor items, matched that of stimuli in a previous target-absent trial, presumably because the current necessary attentional biases were inconsistent with the classification of prior stimuli. Under these circumstances, the right supramarginal gyrus, (sometimes referred to as the temporal parietal junction, or TPJ; Vossel et al., 2009) and the right middle frontal gyrus were substantially increased. These regions are widely considered to be part of the ventral attentional system, believed to play a critical role in regulating attentional biases in the face of current stimulus conditions (Corbetta et al., 2000; Corbetta & Shulman, 2002; Corbetta et al., 2008; Shulman et al., 2003; Shulman et al., 2007); in our paradigm, they were sensitive to the demands of changing the attentional status of a stimulus category. Specifically, when the current target category matches the category of stimuli rejected on a prior target-absent trial, instantiating attentional biases appropriate to the current stimulus environment is more difficult and activation in the ventral attentional system consequently increases.

Our investigation of whether biases against a prior no-target category might be instantiated during perceptual processing yielded no significant results. If target-absent trials' influence on responses to subsequent target items reflected residual suppression of the perceptual processing of the no-target category, we would expect to see FFA response to the current trial to be reduced if that trial were preceded by three faces and PPA response to the current trial to be reduced if that trial were preceded by three houses. We did not find any difference between these conditions. These are, of course, null results, and as such cannot be used to argue forcibly against a purely perceptual explanation of the DPE. They are in line with behavioral work showing that most (if not all) of the DPE is exerted as a difficulty to orient to the target, when the target belongs to the category of items in the preceding target-absent trial. This has been shown using manual responses (Lleras, et al., 2008), a saccadic selection task (Caddigan & Lleras, 2010), RSVP task (Lleras, Kawahara & Levinthal, 2009) and by modeling saccade performance in a pop-out task as an attentional decision making task (Tseng et al., 2014). The current results are therefore consistent with the larger literature in which the DPE is better understood as an attentional than a perceptual bias.

The influence of previous experience on current attentional behavior is of growing interest to cognitive psychologists; here, we find that the VAN is sensitive to trial history. A number of models of attentional control suggest that selection is controlled by a "salience map," through which the perceptual salience and task congruence of an item determines the likelihood that it will guide behavior (Wolfe et al., 1989; Desimone & Duncan, 1995; Itti & Koch, 2000; Cutzu & Tsotsos, 2003; Reynolds & Heeger, 2009). Neurally, perceptual salience is thought to reflect an item's relative dominance of evoked sensory signal, while task goals are represented by prefrontal cortex (Desimone & Duncan, 1995; Reynolds & Heeger, 2009); interactions

between these system determine the extent to which any given item will dominate behavior. More recently, cognitive models have been modified to include selection history as an additional source of attentional bias (e.g. Awh et al., 2012). Both our data and those from the POP paradigm suggest that the dorsal and ventral attentional networks may maintain complementary components of selection history, allowing it to interact with both representational processing in sensory cortex and task-goal instantiation in prefrontal cortex (Desimone & Duncan, 1995; Reynolds & Heeger, 2009).

When considered in conjunction with those of other researchers, our findings suggest that just as the neural systems that instantiate attentional biases and those that evaluate the current stimulus environment's concordance with these biases are dissociated, so too are the systems that maintain an "historical record" of these acts. The POP paradigm does not typically isolate these history effects from one another; both should therefore be reflected in the results of the previous neuroimaging work with the POP (Kristjansson et al., 2007). Specifically, the covariation of targets and non-targets across POP trials should cause covariation in both attentional biases and their relationship to current stimulus items which should in turn produce similar history effects in the dorsal and ventral attentional system. As mentioned in the introduction, exactly such a pattern of results occurs (Kristjansson et al., 2007). Target and non-target feature switches strongly increased activation in both the dorsal and ventral attentional systems, although only the findings from the dorsal attentional system were broadly discussed. The DPE, in contrast, can reflect only the consequences of a current target item having been previously rejected as such. Specifically, no attentional biases towards a target item can be maintained from a "target absent" trial because no target is selected. We found the ventral attentional system to be specifically sensitive to the need to bias attention in favor of current stimuli that were rejected on a previous

trial. We suggest that the dorsal system may be more strongly influenced by prior attentional biases used to select target items while the ventral system may be more strongly influenced by the prior attentional status of a current stimulus item. This is, of course, perfectly consistent with the differential roles putative played by these two systems in maintaining the information that will best meet "top-down" attentional goals and segregating the extent visual scene according to that information.

What is new, however, is our demonstration that trial history, and more specifically, the history of non-target features is handled dynamically by the ventral system: on every trial, information about non-target features is encoded and used to reject those items from selection on both the current and subsequent trials. This processing is entirely goal dependent and specifically linked to the act of attentional selection (or the absence of such selection): (1) when participants are merely asked to detect the presence/absence of an oddball on the display (i.e., detection without localization), no DPE is observed in either RT or accuracy (Caddigan & Lleras, 2010; Lleras et al., 2008); (2) the DPE is observed when participants do not move their eyes and is indexed by the N2PC an electrophysiological marker of selection (Shin et al., 2008); (3) when the non-target features are interpreted as associated with the successful completion of a different behavioral task, their repetition can actually facilitate performance (Lleras, Kawahara & Levinthal, 2009); and (4) the repetition of features that are irrelevant to defining the target in a task do not produce a DPE (Leventhal & Lleras, 2008). Together with the current fMRI results, the evidence strongly suggests that the ventral stream evaluates current stimulus items with respect to both their current and previous attentional status (see Awh et al., 2012). More specifically, the ventral stream is responsible for implementing attentional biases that segregate visual information that does not promote a successful act of selection from that that does. The

ventral system thus plays a complementing role to the dorsal attentional system, which is engaged in biasing attention to facilitate the repetition of successful acts of selection (Kristjannson et al., 2007).

References

Ariga, A., & Kawahara, J. (2004). The perceptual and cognitive distractor-previewing effect. *Journal of Vision*, *4*(10). doi:10.1167/4.10.5

Asplund, C. L., Todd, J. J., Snyder, A. P., & Marois, R. (2010). A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. *Nature neuroscience*, *13*(4), 507–512. doi:10.1038/nn.2509

Astle, D. E., Nixon, E., Jackson, S. R., & Jackson, G. M. (2012). Neural correlates of changing intention in the human FEF and IPS. *Journal of neurophysiology*, *107*(3), 859–867. doi:10.1152/jn.00604.2011

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends in cognitive sciences*, *16*(8), 437–443. doi:10.1016/j.tics.2012.06.010

Bichot, N P, & Schall, J. D. (1999). Effects of similarity and history on neural mechanisms of visual selection. *Nature neuroscience*, *2*(6), 549–554. doi:10.1038/9205

Bichot, Narcisse P, & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *22*(11), 4675–4685. doi:20026410

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial vision*, *10*(4), 433–436.

Caddigan, E., & Lleras, A. (2010). Saccadic repulsion in pop-out search: how a target's dodgy history can push the eyes away from it. *Journal of vision*, *10*(14), 9. doi:10.1167/10.14.9

Corbetta, M, Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature neuroscience*, *3*(3), 292–297. doi:10.1038/73009

Corbetta, Maurizio, Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron*, *58*(3), 306–324. doi:10.1016/j.neuron.2008.04.017

Corbetta, Maurizio, & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature reviews. Neuroscience*, *3*(3), 201–215. doi:10.1038/nrn755

Cutzu, F., & Tsotsos, J. K. (2003a). The selective tuning model of attention: psychophysical evidence for a suppressive annulus around an attended item. *Vision research*, *43*(2), 205–219.

Cutzu, F., & Tsotsos, J. K. (2003b). The selective tuning model of attention: psychophysical evidence for a suppressive annulus around an attended item. *Vision research*, *43*(2), 205–219.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, *18*, 193–222. doi:10.1146/annurev.ne.18.030195.001205

Ellison, A., Schindler, I., Pattison, L. L., & Milner, A. D. (2004). An exploration of the role of the superior temporal gyrus in visual search and spatial perception using TMS. Brain, 127(10), 2307-2315.=

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: recognition, navigation, or encoding? *Neuron*, *23*(1), 115–125.

Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects. *Nature neuroscience*, *2*(6), 568–573. doi:10.1038/9224

Goolsby, B. A., Grabowecky, M., & Suzuki, S. (2005). Adaptive modulation of color salience contingent upon global form coding and task relevance. *Vision research*, *45*(7), 901–930. doi:10.1016/j.visres.2004.10.003

Huang, L., Holcombe, A. O., & Pashler, H. (2004). Repetition priming in visual search: Episodic retrieval, not feature priming. *Memory & Cognition*, *32*(1), 12–20. doi:10.3758/BF03195816

Inter-trial inhibition of attention to features is modulated by task relevance. (n.d.). Retrieved July 25, 2013, from http://w.journalofvision.org/content/8/15/12.short

James, W. (1918). *The Principles of Psychology*. H. Holt.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*(2), 825–841.

Kanwisher, N., Stanley, D., & Harris, A. (1999). The fusiform face area is selective for faces not animals. *Neuroreport*, *10*(1), 183–187.

Kastner, S, Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*(4), 751–761.

Kastner, Sabine, DeSimone, K., Konen, C. S., Szczepanski, S. M., Weiner, K. S., & Schneider, K. A. (2007). Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. *Journal of neurophysiology*, *97*(5), 3494–3507. doi:10.1152/jn.00010.2007

Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *The Journal of*

neuroscience: the official journal of the Society for Neuroscience, *25*(18), 4593–4604. doi:10.1523/JNEUROSCI.0236-05.2005

Kristjánsson, A., Vuilleumier, P., Malhotra, P., Husain, M., & Driver, J. (2005). Priming of color and position during visual search in unilateral spatial neglect. *Journal of cognitive neuroscience*, *17*(6), 859–873. doi:10.1162/0898929054021148

Kristjánsson, A., Vuilleumier, P., Schwartz, S., Macaluso, E., & Driver, J. (2007). Neural basis for priming of pop-out during visual search revealed with fMRI. *Cerebral cortex (New York, N.Y.: 1991)*, *17*(7), 1612–1624. doi:10.1093/cercor/bhl072

Levinthal, B. R., & Lleras, A. (2008). Inter-trial inhibition of attention to features is modulated by task relevance. *Journal of Vision*, *8*(15). doi:10.1167/8.15.12

Lleras, A., Kawahara, J., & Levinthal, B. R. (2009). Past rejections lead to future misses: Selection-related inhibition produces blink-like misses of future (easily detectable) events. *Journal of Vision*, *9*(3). doi:10.1167/9.3.26

Lleras, A., Kawahara, J.-I., Wan, X. I., & Ariga, A. (2008). Intertrial inhibition of focused attention in pop-out search. *Perception & Psychophysics*, *70*(1), 114–131. doi:10.3758/PP.70.1.114

Lleras, A., Levinthal, B. R., & Kawahara, J. (2009). The remains of the trial: goal-determined inter-trial suppression of selective attention. In Narayanan Srinivasan (Ed.), *Progress in Brain Research* (Vol. Volume 176, pp. 195–213). Elsevier. Retrieved from http://www.sciencedirect.com/science/article/pii/S0079612309176112

Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, *22*(6), 657–672. doi:10.3758/BF03209251

Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, *58*(7), 977–991. doi:10.3758/BF03206826

Manoach, D. S., Thakkar, K. N., Cain, M. S., Polli, F. E., Edelman, J. A., Fischl, B., & Barton, J. J. S. (2007). Neural activity is modulated by trial history: a functional magnetic resonance imaging study of the effects of a previous antisaccade. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *27*(7), 1791–1798. doi:10.1523/JNEUROSCI.3662-06.2007

Mitchell, D. J., & Cusack, R. (2008). Flexible, capacity-limited activity of posterior parietal cortex in perceptual as well as visual short-term memory tasks. *Cerebral cortex (New York, N.Y.: 1991)*, *18*(8), 1788–1798. doi:10.1093/cercor/bhm205

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial vision*, *10*(4), 437–442.

Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, *61*(2), 168–185. doi:10.1016/j.neuron.2009.01.002

Saccadic repulsion in pop-out search: how a target's d... [J Vis. 2010] - PubMed - NCBI. (n.d.). Retrieved September 19, 2013, from http://www.ncbi.nlm.nih.gov/pubmed/21135256

Scalf, P. E., Basak, C., & Beck, D. M. (2011). Attention does more than modulate suppressive interactions: attending to multiple items. *Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale*, *212*(2), 293–304. doi:10.1007/s00221-011-2730-z

Scalf, P. E., & Beck, D. M. (2010). Competition in visual cortex impedes attention to multiple items. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *30*(1), 161–169. doi:10.1523/JNEUROSCI.4207-09.2010

Serences, J. T., Shomstein, S., Leber, A. B., Golay, X., Egeth, H. E., & Yantis, S. (2005). Coordination of Voluntary and Stimulus-Driven Attentional Control in Human Cortex. *Psychological Science*, *16*(2), 114–122. doi:10.1111/j.0956-7976.2005.00791.x

Shin, E., Wan, X. I., Fabiani, M., Gratton, G., & Lleras, A. (2008). Electrophysiological evidence of feature-based inhibition of focused attention across consecutive trials. *Psychophysiology*, *45*(5), 804–811. doi:10.1111/j.1469-8986.2008.00679.x

Shulman, G. L., Astafiev, S. V., McAvoy, M. P., D' Avossa, G., & Corbetta, M. (2007). Right TPJ deactivation during visual search: functional significance and support for a filter hypothesis. *Cerebral cortex (New York, N.Y.: 1991)*, *17*(11), 2625–2633. doi:10.1093/cercor/bhl170

Shulman, G. L., McAvoy, M. P., Cowan, M. C., Astafiev, S. V., Tansy, A. P., D' Avossa, G., & Corbetta, M. (2003). Quantitative analysis of attention and detection signals during visual search. *Journal of neurophysiology*, *90*(5), 3384–3397. doi:10.1152/jn.00343.2003

Smith, S. M. (2002). Fast robust automated brain extraction. *Human brain mapping*, *17*(3), 143–155. doi:10.1002/hbm.10062

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., … Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, *23 Suppl 1*, S208–219. doi:10.1016/j.neuroimage.2004.07.051

Suzuki, M., & Gottlieb, J. (2013). Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. *Nature Neuroscience*, *16*(1), 98–104. doi:10.1038/nn.3282

Szczepanski, S. M., Konen, C. S., & Kastner, S. (2010). Mechanisms of spatial attention control in frontal and parietal cortex. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *30*(1), 148–160. doi:10.1523/JNEUROSCI.3862-09.2010

Szczepanski, S.M., Pinsk, M.A., Douglas, M.M., Kastner, S., Saalmann, Y.B. (2013) Functional and structural architecture of the human dorsal frontoparietal attention network. *Proceedings of the National Academy of Sciences, 110 (39),* 15806-11. doi: 10.1073/pnas.1313903110.

Todd, J. J., Fougnie, D., & Marois, R. (2005). Visual short-term memory load suppresses temporo-parietal junction activity and induces inattentional blindness. *Psychological science*, *16*(12), 965–972. doi:10.1111/j.1467-9280.2005.01645.x

Wolfe, J M, Cave, K. R., & Franzel, S. L. (1989). Guided search: an alternative to the feature integration model for visual search. *Journal of experimental psychology. Human perception and performance*, *15*(3), 419–433.

Wolfe, Jeremy M., Butcher, S. J., Lee, C., & Hyle, M. (2003). Changing your mind: On the contributions of top-down and bottom-up guidance in visual search for feature singletons. *Journal of Experimental Psychology: Human Perception and Performance*, *29*(2), 483–502. doi:10.1037/0096-1523.29.2.483

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage*, *14*(6), 1370–1386. doi:10.1006/nimg.2001.0931

Xu, Y., & Chun, M. M. (2007). Visual grouping in human parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(47), 18766–18771. doi:10.1073/pnas.0705618104

Zhou, H., & Desimone, R. (2011). Feature-based attention in the Frontal Eye Field and area V4 during visual search. *Neuron*, *70*(6), 1205–1217. doi:10.1016/j.neuron.2011.04.032